

**Behavioral Studies of Three Morphotypes of
*Therion circumflexum***

(Hymenoptera: Ichneumonidae)

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Therion is a genus of wasps that are parasitoids of Lepidoptera caterpillars. The female lays an egg into the body cavity of a host caterpillar; the egg develops into a larva that feeds on the host's non-vital tissues. Eventually the host pupates, at which time the parasitoid larva kills the host, pupates inside the host's pupal shell, and emerges from the pupal shell as an adult wasp. It has recently been shown that all North American *Therion* can be considered as members of a single species, *T. circumflexum* (L.), with distinct groups of populations that can be segregated into ten separate morphological types or morphotypes (Slobodchikoff, 1971). The purpose of the present paper is to report on the behavior of three of the ten morphotypes.

The behavior of the three morphotypes, CIRCUMFLEXUM, CALIFORNICUM, and MORIO was studied both in the field and in the laboratory. When this study was begun, it was expected that minor differences would be observed between morphotypes in most of the behavioral categories described in the present paper. However, observation and experimentation demonstrated that all three morphotypes have the same behavioral response patterns in every category except host selection.

MATERIALS AND METHODS

The materials and methods used in the behavioral studies were the following. CALIFORNICUM adults were observed while contained in a sleeve cage, 0.5 m on each side with a fine wire mesh. CIRCUMFLEXUM and MORIO adults were observed while contained in transparent plastic shoeboxes and in half-gallon ice cream cartons covered with a piece of 2 mm-thick glass. The shoeboxes had their ends cut off and substituted by a fine wire mesh. The top of each shoebox had a 5 × 6 cm mesh to insure proper ventilation and had three circular holes, each measuring 2.5 cm in diameter, for introducing food, water, and experimental items. These circular holes were normally plugged with cotton. Wasp parts were weighed on a Mettler balance to the nearest 0.05 mg. Potter's clay was used for constructing the model of

the insect in flight. The model was baked in a Braun oven at 40° C for 24 hours, then allowed to cool for 24 hours. The response to light was tested with an American Optical Company microscope illuminator and a gooseneck desk lamp with a 100 watt bulb. Temperature was measured by a Celsius thermometer and by a hygrothermograph. Temperature in the laboratory remained at $20 \pm 2^\circ$ C, relative humidity averaged 40 per cent. Mating was observed in part while the wasps were caged in a 90 × 30 mm glass vial with a cotton plug at the top.

RESULTS AND DISCUSSION

HABITATS STUDIED.—Extensive field observations of CIRCUMFLEXUM'S behavior were made at Lily Lake, Marin County, California. Lily Lake is situated in the California Coast Ranges, and is surrounded by hills and ridges with narrow canyons containing seasonal streams. The habitat around Lily Lake may be characterized as grassland along the tops of ridges, oak-chaparral woodland among the slopes of the hills, and mixed evergreen-redwood forest along the canyon floors. CIRCUMFLEXUM was found only in the oak-chaparral areas. Individuals of this morphotype were typically seen flying around oaks and in the grass surrounding oak trees. Specimens of CALIFORNICUM were collected from similar habitats in areas near Lily Lake. Observations of the behavior of CALIFORNICUM were made at Hallelujah Junction, Lassen County, California, and at a cotton field near Kerman, Kern County, California. Hallelujah Junction has a Great Basin flora and fauna. *Therion* individuals were found flying around willows along a stream. The cotton field near Kerman was, at the time the observations were made, an experimental plot for control of bollworm (*Heliothis zea* (Boddie)) by *Bacillus thuringiensis* Berliner, and had not been sprayed with insecticides for the previous two years.

The behavior of MORIO was observed at Verdi, Washoe County, Nevada, in a patch of willows along the Truckee River. The habitat around Verdi may also, like Hallelujah Junction, be characterized as Great Basin. Only three females and four males were found at this locality during two days of observation. No other *Therion* were found in surrounding willow patches for half a mile in either direction along the Truckee River. The Verdi colony is probably an isolated one with a low population density.

In California, the three morphotypes are often found in the vicinity of willows. CALIFORNICUM is also found in cotton and alfalfa fields. In addition to willows, CIRCUMFLEXUM is found near oaks

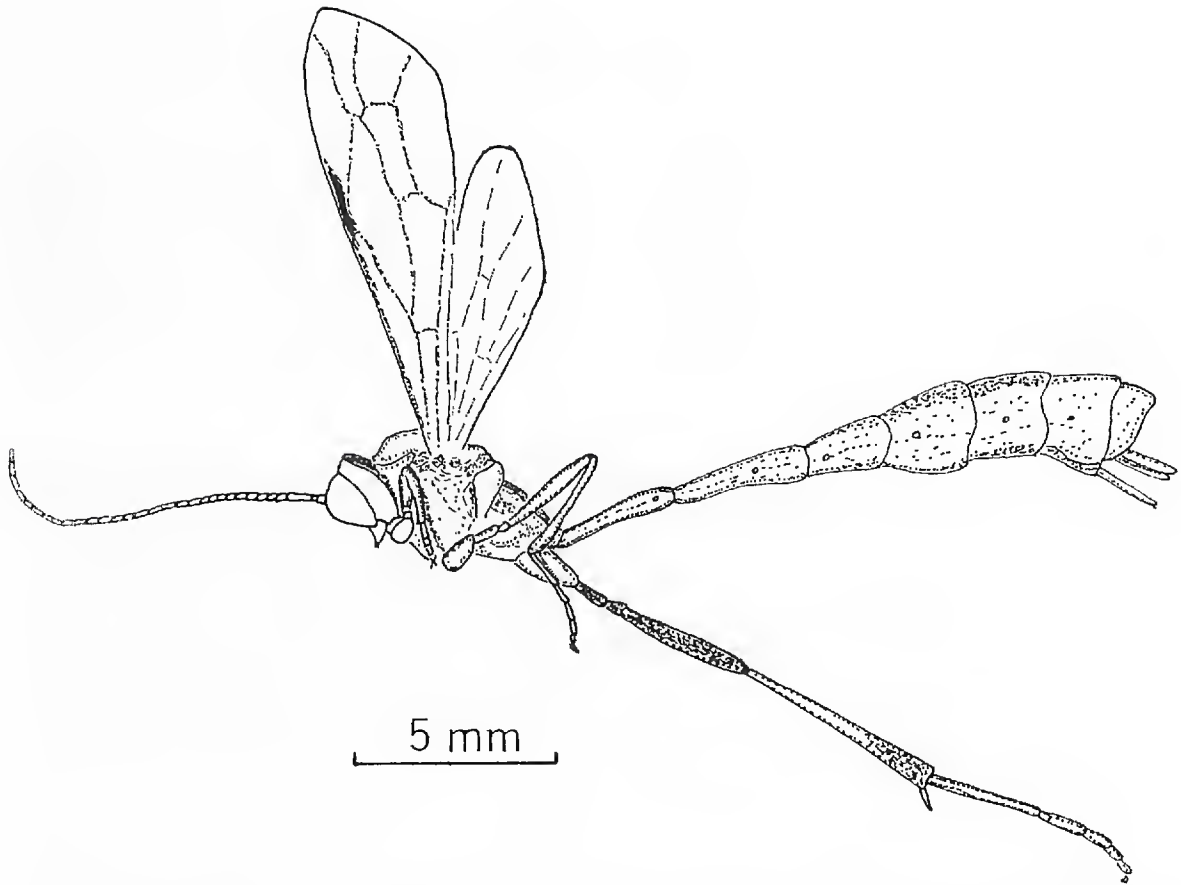


FIG. 1. Female *T. circumflexum* in flight. Adapted from a 35 mm photograph.

in oak-woodland habitats. MORIO has only been recorded from habitats containing willows. In all observed cases, the *Therion* lived in isolated colonies. At a given locality, all the *Therion* individuals were found within a small area, often less than one square mile in size. Outside of this area, no *Therion* were found, although the habitat was quite similar in surrounding areas.

FLIGHT.—*Therion* males and females characteristically fly with the abdomen elevated and the hind legs outstretched (Fig. 1). Sometimes the middle and front pairs of legs are extended to the sides, with the femora pointed laterally away from the thorax and the tibiae and tarsi pointed downward. As the wasp flies, the abdomen may be seen to occasionally move up or down. This movement follows a change in the position of the thorax relative to a horizontal plane. If the thorax dips forward, so that the head is lowered and the propodeum is raised, the abdomen moves down. If the thorax dips backwards, so that the head is raised and the propodeum is lowered, the abdomen moves up. If an imaginary plane is extended through the thorax while the wasp is in flight, so that half of the thorax is above this plane and half is below, the abdomen is held at a 20 degree angle above the plane and the legs are held at a 20 degree angle below the plane.

Table 1. Measurements of body parts of a male *circumflexum*.

Part	Weight mg	Dimensions mm (l × h × w)	Volume mm ³
Head	2.75	1.3 × 1.7 × 2.0	4.42
Thorax and wings	12.40	6.0 × 3.0 × 3.0	54.00
Abdomen	9.00	16.0 × 2.2 × 0.8	26.40
Hind legs	2.55	17.5 × 0.5 × 0.5	4.38

The wasp in flight may be considered as three separate arms balanced around a center of gravity. The thorax, head, wings, and first two pairs of legs comprise one arm. The hind pair of legs comprise the second arm, and the abdomen comprises the third arm. On the basis of observations of the movement of these arms, the center of gravity of the wasp in flight may be predicted to be at the point where the arms join, near the hind end of the propodeum. If the head pitches forward or backward, the center of gravity shifts. To compensate for the shift, the abdomen moves either up or down, bringing the center of gravity back to the end of the propodeum.

To see whether the center of gravity of a wasp is actually at the end of the propodeum, an experiment using a clay model was performed. A male CIRCUMFLEXUM, freshly killed, was cut into the following parts: (1) the head; (2) the thorax, wings, and first two pairs of legs; (3) the abdomen, including the petiole; and (4) the hind legs, including the coxae. These four parts were weighed and were measured. The volume of each part was calculated. The data obtained from these measurements are summarized in Table 1. A scale model was made, attempting to reproduce the actual contours of the wasp as closely as possible. The scaling factor for the weight was 1×10^3 , and the factor for the dimensions was 0.5×10 . The abdomen and legs were fixed at 20 degree angles with respect to the horizontal plane. When the model was suspended by a string tied around the juncture of the abdomen, legs, and thorax, the model balanced in the position that the wasp uses for level flight.

RESTING AND GROOMING.—In both the laboratory and in the field, *Therion* adults may frequently be observed at rest clinging to an object in a head-upright position perpendicular to the ground, and either remaining motionless or cleaning portions of the body. Cleaning consists of a series of actions. First one antennal flagellum, then the other, is drawn through the space between the strongly curved front tibial spur

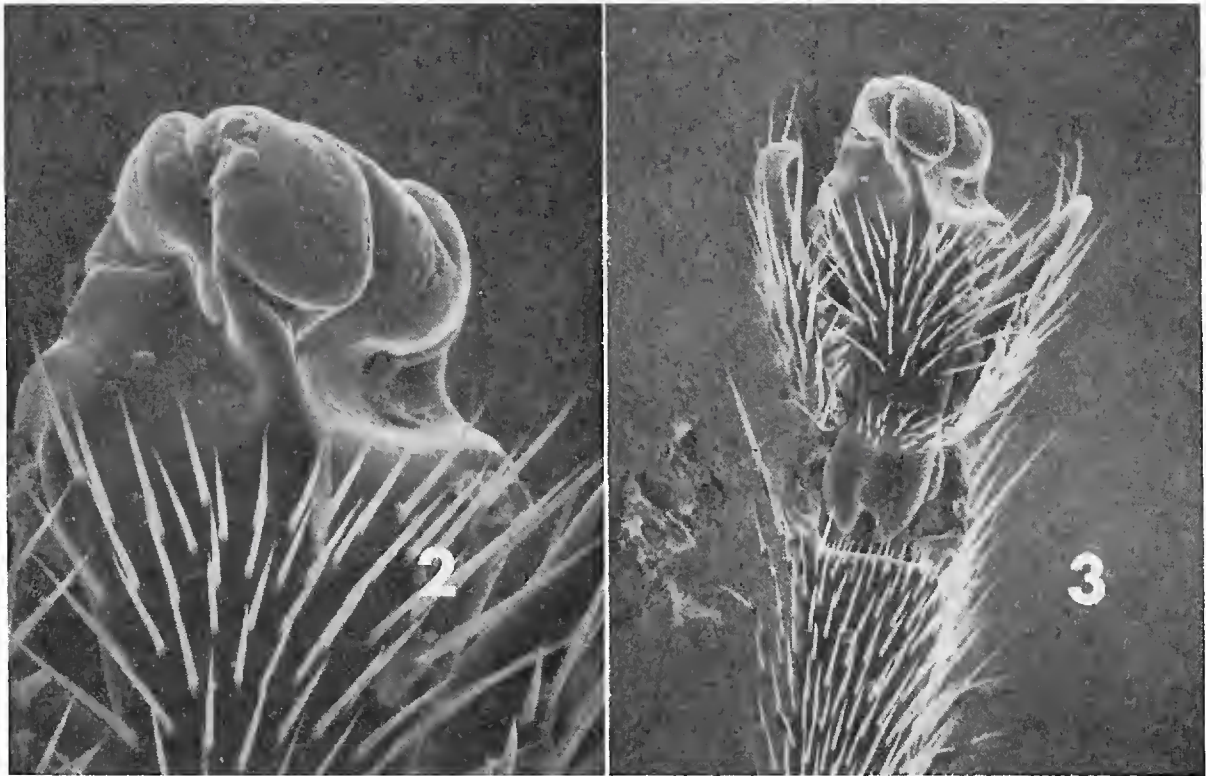


FIG. 2. Spongy empodium between tarsal claws of *T. circumflexum*. Scanning electron micrograph, 420 $\times$. FIG. 3. Tarsal pad and spongy empodium, tarsal segments 4-5 of *T. circumflexum*. Scanning electron micrograph, 170 $\times$.

and the first tarsal segment. The right front leg cleans the right flagellum, while the left front leg cleans the left one. The tibial spur and the front tarsal segments are then brushed against the mouthparts, each leg brushing the mouthparts on its own side. Following this, the tarsal segments and tibial spur of the middle leg are brushed against the end of the tibia and the tarsal segments of the front leg. The same action is repeated by the hind legs, brushing against the tibia and tarsal segments of the middle leg. Then the wings are held out flat on either side of the abdomen, with their upper surfaces parallel to the dorsum of the wasp. The tibia of one hind leg brushes against the surface of the other two wings. After cleaning the wings, the hind legs are used to brush the posterior half of the abdomen. This is accomplished by simultaneously moving the tarsal segments and tibial spurs of each hind leg along the sides of the abdomen toward the posterior end. The abdomen-brushing action is usually repeated 2-3 times. Cleaning behavior concludes with the brushing of the tibial spur and lower surfaces of the tarsal segments on one hind leg against the upper surface of the other leg's tarsal segments, then a corresponding action for brushing the segments of the other leg.

Therion adults often cling to blades of grass or small twigs during resting in the field. In the laboratory they are capable of clinging to

glass and smooth plastic as well as to materials such as twigs, paper towels, and wire meshes. Clinging to smooth surfaces is facilitated by a large, spongy, empodium (Fig. 2) on the pretarsus and by four tarsal pads per leg. Each tarsal pad lies in the intersegmental space between tarsal segments, and appears to overlap the segment distal to it (Fig. 3). The pad consists of spongy ridged tissue that, when pressed against a smooth surface, has a suction effect. The empodium also functions as a suction pad.

RESPONSE TO LIGHT.—Both males and females of the three morphotypes exhibit positive phototaxis. If given an intensity gradient of light, the wasps will move to the area of greatest intensity. A simple experiment was performed to establish this. Eight males and ten females of *CIRCUMFLEXUM* were confined in a plastic cage. The cage was placed in a darkened room at 9 p.m., PDT, for one hour. A microscope illuminator, set at low intensity (300 ft. candles at the end of the cage nearest light, 100 ft. candles at the middle of the cage), was placed one foot from one end of the cage. The illuminator was positioned so that the beam of light would pass along the length of the cage. At the end of one hour, the illuminator was switched off. Initially, the *Therion* were distributed fairly uniformly in the cage, all in resting positions. However, within five seconds of application of the light stimulus, movement was elicited. Within 30 seconds, seven males and all ten females had crawled or flown to the side of the cage closest to the light. Within one minute, all the individuals were along that side. This experiment was repeated three times on separate days. In each case, all individuals were along the side closest to the light within one minute. The wasps showed no habituation to the light, and remained at the side of the cage nearest to the light until the light was switched off.

The same experiment was performed with four males and three females of *MORIO*, under similar experimental conditions. In three replicates, on separate days, the same results as with *CIRCUMFLEXUM* were obtained. *CALIFORNICUM* males and females were found to respond in a similar fashion to a desk lamp after a period of darkness. If a diffuse light, such as that produced by an overhead white fluorescent lamp, was switched on after a period of darkness, and the intensity gradient was comparatively low, the wasps of all three morphotypes became active within one minute. However, they did not congregate at any given side of the cage.

RESPONSE TO TEMPERATURE.—Both *CALIFORNICUM* and *CIRCUMFLEXUM* become increasingly active with temperatures higher than

ca. 15 degrees C. CALIFORNICUM adults at Hallelujah Junction and near Kerman begin to appear about 7:30 or 8:00 a.m., PDT, when the temperature begins to exceed 17 degrees C. CALIFORNICUM adults near Lily Lake, where temperatures are generally cooler, become active later in the day, around 9:30 or 10:00 a.m., PDT, when the temperature begins to exceed 15 degrees C. On sunny warmer mornings, CIRCUMFLEXUM adults at Lily Lake become active earlier than on cooler sunny mornings. The same response to temperature has been reported for eastern MORIO by Tothill (1922).

MATING.—The mating behavior of CALIFORNICUM and CIRCUMFLEXUM was observed in the laboratory, but not in the field. The mating behavior of MORIO was not observed. CALIFORNICUM was observed mating on two occasions, one while the individuals were confined in the plastic cage described above, and one while the individuals mating were confined in a glass vial.

Both morphotypes go through the same set of actions for mating. Tothill (1922) reports that MORIO mates by pairing in flight and falling to the ground. No pairing in flight was observed for the two morphotypes studied, but that may be a consequence of laboratory confinement. In both morphotypes, the male approaches the female from the rear and moves his antennae along the posterior half of her abdomen 2–5 times. He then climbs onto her dorsum, curls his abdomen around so that the tip of the genital capsule is pointing anteriorly, and couples with her.

The male and female remain coupled for 1–2 minutes (55 and 104 seconds for CALIFORNICUM, 70 and 78 seconds for CIRCUMFLEXUM), following which the female immediately flies off. The male, however, remains motionless for about another minute (45 and 62 for CALIFORNICUM, 48 and 75 seconds for CIRCUMFLEXUM). In all four observed matings, the male assumed the characteristic position taken by wasps at death. The wings were partially spread to the sides and depressed, the abdomen was partially curled underneath itself, and the legs were spread to the sides. The CIRCUMFLEXUM individuals were field collected and it is not known if any sperm was transferred during the observed matings, but the CALIFORNICUM individuals were laboratory reared, and gave rise to female progeny. Tothill (1922) reports that in two observed matings of MORIO, the individuals remained coupled for five and fifteen minutes respectively.

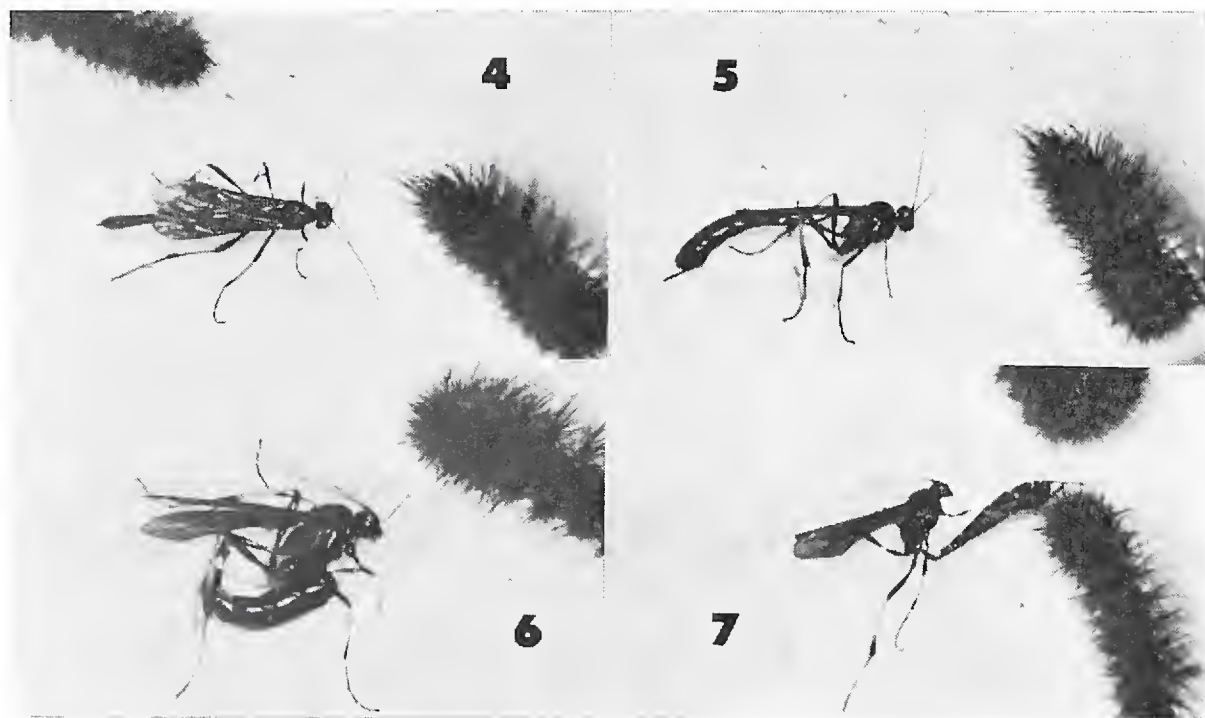
FEEDING AND DRINKING.—In the laboratory males and females readily accept either a diet of clover honey mixed with tap water in a 1:1 proportion or a diet of pure clover honey. These diets provide sufficient

nutrients for the wasps to produce viable progeny. With either diet, water is the only other requirement. Wetting a piece of cotton in the cage is a convenient way of providing the water, since the wasps can easily extract the absorbed liquid. Water has to be provided daily. When three laboratory-reared, newly emerged individuals of CALIFORNICUM were fed diluted honey but were deprived of pure water, all three wasps were found dead at the end of 36 hours. The general characteristics of drinking behavior in ichneumonids have been discussed by Townes (1958). Tothill (1922) found that adults of MORIO in the eastern United States eat pollen grains of goldenrod in the field, and will eat sugar mixed with water, the fresh inside of a banana skin, or pollen grains of goldenrod in the laboratory. The adults of CALIFORNICUM and CIRCUMFLEXUM probably also normally feed on pollen grains.

HOST SEARCHING AND SELECTION.—When searching for hosts, females of all three morphotypes characteristically fly in slow zigzags not more than 1.5 meters above the ground. Periodically, a female will alight on a twig, leaf, or grass stem and explore the surrounding area within a 15 cm radius. During such explorations, the antennae are moved up, down, and from side to side, frequently touching the substrate on which the female is walking. Following a local exploration, the female resumes her zigzag pattern of flight.

The factors involved in host selection have been described elsewhere (Slobodchikoff, 1971). Odor provides an important initial cue that allows the wasps to find a potential host. Once the host is located, a female uses tactile cues provided by the surface of the caterpillar. The hosts of CIRCUMFLEXUM and CALIFORNICUM have no secondary setae on the integument, while the hosts of MORIO have dense patches of secondary setae. A female of all three morphotypes will approach a potential host and extend her antennae to the caterpillar's surface, briefly touching the caterpillar. If a MORIO female encounters an integument bare of patches of secondary setae, she loses all further interest in the caterpillar as a potential host. Similarly, females of CIRCUMFLEXUM and CALIFORNICUM lose all interest in a potential host, even in the presence of the proper odor, if an antennal scan of the surface encounters anything other than a wrinkled integument free of secondary setae. Even when a female wasp is deprived of suitable hosts for prolonged periods of time, caterpillars with improper cues are rejected as hosts.

OVIPOSITION.—Oviposition behavior begins when the wasp encounters a suitable host. In all three morphotypes studied, oviposition follows



FIGS. 4-7. Oviposition behavior sequence of female *T. circumflexum*, morphotype MORIO, in response to a woolly bear caterpillar, *Estigmene acrea* Drury. In this particular sequence, the female wasp misjudged the position of the caterpillar. See text for further explanation.

the same pattern. With her antennae held above her head, the female approaches to within 1.0–1.5 cm of the larva. She taps either the larval integument (if the larva is relatively hairless) or several larval hairs (if the larva is hairy) a few times with her antennae (Fig. 4). Then the antennae are raised above the head again. The abdomen is curled under the thorax so that the tip of the ovipositor is below and slightly in front of the head (Fig. 5). The abdomen fits between the hind coxae, which are pressed against the sides of the abdomen. The wasp typically cants her body to either her right or her left side, so that the dorsum of the wasp is held at approximately 45 degrees relative to the substrate on which the wasp is standing (Fig. 6). This allows her to rapidly extend the abdomen without interference from the substrate. If she decides to sting the host, the entire abdomen is rapidly thrown forward and the ovipositor pierces the larval integument. With the extension of the abdomen, the thorax is pulled up and back, and the first two pairs of legs are lifted from the surface of the substrate (Fig. 7). Actual egg-laying, from the time the abdomen is thrust forward, takes less than one second. The ovipositor penetrates to the body wall opposite the point of entry. This was first recorded by Tothill (1922) as characteristic of egg-laying by MORIO. After ovipositing, the female usually cleans herself.

CONCLUSIONS

The similarities and differences of behavioral patterns can be interpreted in terms of selection pressure and partitioning of the environment. All three morphotypes are sympatric, in the broad sense, through at least part of their range (Slobodchikoff, 1971). However, populations of the three morphotypes are usually small, with each population distributed over less than two square miles. Populations of the different morphotypes generally do not overlap, so that functionally the morphotypes are microallopatric. At the same time, populations of different morphotypes may be separated by as little as two miles, and may occur in the same type of habitat. Fluctuations in population size may bring two different morphotypes into contact, in which case it would be advantageous to insure maximum survival of progeny. Selection would be expected to have a disruptive effect on host preferences, and a neutral effect on all behavioral patterns not directly connected with the survival of offspring.

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